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TITLE Biomass and nutrients in aboveground vegetation and soils of Florida oak-saw palmetto scrub.	AUTHOR(S) Schmalzer, P.A. and C.R. Hinkle.
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Biomass and Nutrients in Aboveground Vegetation and Soils of Florida Oak-Saw Palmetto Scrub

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ABSTRACT

We sampled aboveground biomass in four stands of oak-saw palmetto scrub vegetation that were 2, 4, 8, and 25 years since the previous fire by harvesting 1 m² plots. Biomass samples were analyzed for major nutrients. We sampled and analyzed soils from the 0-15 cm and 15-30 cm layers. Stands were dominated by *Quercus myrtifolia*, *Q. geminata*, *Q. chapmanii*, *Serenoa repens*, and ericaceous shrubs. Live aboveground biomass (excluding saw palmetto rhizomes) increased with time since fire. Litter biomass increased for eight years after fire. Standing dead biomass was an important component of aboveground biomass throughout the time sequence. Aboveground saw palmetto rhizomes were a major biomass category. Nutrient concentrations in live aboveground biomass did not appear to change with time since fire and were similar to those in other shrublands. Biomass pools of major nutrients frequently equaled or exceeded those in the soil, but wetter sites had more organic matter and nutrients in the soil. Atmospheric deposition of N, P, Ca, Mg, and K was low compared to biomass pools. Retention of nutrients in soils and regrowing vegetation after fire may be important to the persistence of scrub on low nutrient soils.

INTRODUCTION

Florida scrub vegetation is characterized by a shrub layer of evergreen, sclerophyllous species including myrtle (*Quercus myrtifolia*), sand live (*Q. geminata*) and Chapman (*Q. chapmanii*) oaks, ericads such as rusty lyonia (*Lyonia ferruginea*), repent palms such as saw palmetto (*Serenoa repens*), and other shrubs such as Florida rosemary (*Ceratiola ericoides*), usually occurring on well-drained, sandy soils low in nutrients, and burning in periodic, intense fires (Muldavia 1931; Webber 1935; Kurz 1942; Laessle 1942, 1958, 1967; Myers 1990). In this paper, we examine oak-saw palmetto scrub vegetation that lacks a tree canopy; a type sometimes termed scrubby flatwoods (Laessle 1942; Abrahamson 1984a, 1984b; Abrahamson et al. 1984; Givens et al. 1984; Abrahamson and Hartnett 1990).

Natural fire frequency for oak-saw palmetto scrub is not known with certainty. It is believed that oak-saw palmetto scrub burned more frequently than sand pine (*Pinus clausa*) scrub, thought to have a fire cycle of 20 to 40 or more years (Austin 1976), and more frequently than rosemary scrub with a fire cycle

years (Johnson 1982), but less often than the two
Pinus palustris)/wiregrass (*Aristida stricta*)
 (Johnson et al. 1984). Burning intervals of 5–20 years
 maintain scrub habitat for the Florida Scrub Jay
Geothlypis trichas (Fitzpatrick et al. 1991).

Guerin (1988, 1993) provide the only other pub-
 lished data on scrub vegetation. Little is known of nutrient
 cycles in scrub and their responses to fire. Vickers
 measured nutrient concentrations for several scrub species
 that evolved under regimes of low nutrient soils
 (Vickers 1984a, 1984b); however, such oligotrophic sys-
 tems suffer losses from fire (Raison 1979, Boerner 1982).
 Losses occur from direct volatilization of organic matter,
 wind or water erosion of ash, and leaching to ground-
 water by fire (Raison 1979, Wells et al. 1979, Raison
 1982). Scrub species may be an adaptation to low nutrient
 soils (Monk 1966) as well as drought stress.

We measured standing crops of biomass and nutrients in an
 experimental scrub stands on Merritt Island, Kennedy Space
 Center on less well drained soils; thus, we also examine
 a nutrient gradient on biomass and nutrients.

METHODS

We selected scrub vegetation that were 2, 4, 8, and 25
 years old for sampling in an inland region of scrub
 (Hinkle and Hinkle 1992). Stand 1 was eight years since
 fire, one to two meters tall. Stand 2 had burned four
 years before sampling. Stand 4 was about 25
 years old. All the transects of Stands 1 and 3 were
 on *Spartina patens*; transects of Stand 4 were on *Pomello*
la sand (Spodic Quartzipsamment) (Huckle et al.
 1992). Two transects were on *Pomello* sand, but two were on the
Aeric Haplaquod. Species composition and
 biomass were measured (Schmalzer and Hinkle (1992)).

Study

We measured biomass, living and dead, and litter on plots
 of vegetation sampling transects used to determine
 biomass (Hinkle and Hinkle 1987, 1992). Material was harvested
 from a quadrat as projected above the ground; sections
 of the plot but extending beyond it were excluded.
 Only above- or below-ground; only the aboveground
 biomass was measured. We did not attempt to separate rhizomes into live and
 dead biomass samples into leaves, stems, trunks
 and rhizomes, and oven-dried them at 105°C to con-
 sider dead biomass were considered, litter biomass

consisting of intact leaves and stems on the ground and standing dead biomass consisting of erect dead stems and attached dead palmetto leaves.

Due to limitations in the number of samples that could be analyzed, we took subsamples from each harvested plot within a stand in which the taxa occurred and pooled them for chemical analyses. Samples were ground, homogenized, and oven-dried at 105°C. For metals and phosphorus analyses, 1 g of oven-dried material was dry-ashed at 450°C in a muffle furnace (Wolfe 1962) and taken up in hydrochloric acid. Analyses for calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), and aluminum (Al) were performed by atomic absorption spectrophotometry (Perkin-Elmer Corporation 1982). Total phosphorus (P) was determined by automated colorimetry (Technicon Industrial Systems 1983b). To determine total Kjeldahl nitrogen (TKN), a 0.25 g sample was digested in 2 ml concentrated H_2SO_4 , 2 ml 30% H_2O_2 , and 4 ml of K_2SO_4 - CuSO_4 digestion mixture in a model BD-40 block digester and analyzed by automated colorimetry (Technicon Industrial Systems 1983a). We calculated standing crops of nutrients in aboveground biomass per plot by multiplying the biomass of the plant part or other biomass category by its nutrient concentration.

Soil and Precipitation Chemistry

We sampled soils from the 0 to 15 cm and 15 to 30 cm depths near each transect. Soil samples were air dried, large roots excluded, homogenized, and then analyzed for pH, organic matter, conductivity, cation exchange capacity, exchangeable Ca, Mg, Na, K, nitrate-nitrogen ($\text{NO}_3\text{-N}$), ammonium-nitrogen ($\text{NH}_4\text{-N}$), TKN, and Al. Methods of soil analyses and concentration data are given elsewhere (Schmalzer and Hinkle 1987, 1992). We calculated standing crops of nutrients per square meter in the soil to a depth of 30 cm from nutrient concentrations and soil bulk density. Based on bulk density data given in soil surveys of Brevard County (Huckle et al. 1974) and Volusia County (Baldwin et al. 1980), we used a bulk density value of 1.20 g/cm³ for the 0 to 15 cm layer and a value of 1.50 g/cm³ for the 15 to 30 cm layer. Mean annual deposition of inorganic nitrogen (N), Ca, Mg, K, and Na was calculated from 10 years of data (1978–87) from the National Atmospheric Deposition Program (NADP) station centrally located on Merritt Island (Madsen et al. 1992).

Data Analysis

Data on biomass, nutrient standing crops, and soil nutrient pools were log-transformed before most analyses to enhance normality. The combined soil nutrient pools (0–30 cm) were compared among the four stands using one-way analysis of variance (ANOVA); the samples occurring on Myakka soils were excluded from this comparison. Previous analyses (Schmalzer and Hinkle 1992) had shown that most nutrients were related to soil organic matter, and Stand 2 had higher organic matter levels even after excluding the Myakka soils. Therefore if the overall ANOVA was significant, a priori contrasts were used to test whether Stand 2 differed from the other stands (Day and Quinn 1989). Biomass nutrient pools for total live leaves, total live stems, standing dead plus litter, and total biomass including saw palmetto rhizomes were compared using one-way ANOVA.

among the four stands of differing ages. The sample size of the vegetation on Myakka soils was not sufficient for statistical comparison to the other data; however, we present data from these samples in tables and figures because they present a useful contrast. Analysis of total nutrient pools in soil and biomass began with two-way ANOVA with stands and source (biomass/soil) as factors; however, two-way interactions were significant for most nutrients. Therefore, t-tests between biomass and soil pools for each stand were used for comparisons. Statistical analyses were conducted with SPSS for Windows (Norusis 1993).

RESULTS

Biomass

Leaves and stems of scrub oaks were the primary components of live biomass excluding saw palmetto rhizomes (Table 1) in all except the saw palmetto-dominated plots of Stand 2. Saw palmetto rhizomes were a major biomass category except in Stand 4. The rhizomes of saw palmetto are fire resistant and form a refractory part of the scrub community. The live biomass category excluded saw palmetto rhizomes when trends over time were being examined. Litter plus standing dead biomass exceeded live biomass except in the oldest stand.

Biomass changed with time since fire. Live biomass increased with time since fire, rapidly at first and then more slowly (Figure 1). The relationship of live biomass with age was best expressed by the equation: $\log_{10} \text{live biomass} = 0.391 \cdot \log_{10} \text{age} + 2.758$, $r = 0.59$, $p = 0.002$. Litter biomass (Figure 2) was highly variable in the most recently burned stand probably due to the patchy intensity of the fire that removed most litter in some places but not others. Litter increased with time to about year 8; the relationship was fit best by the equation: $\log_{10} \text{litter biomass} = 0.558 \cdot \log_{10} \text{age} + 2.364$, $r = 0.60$, $p = 0.002$. Standing dead biomass was highly variable in the recently burned stand (Figure 3). It showed no trend with time ($r = 0.12$, $p = 0.56$). The composition of standing dead biomass changed with time (personal observation). In the most recently burned stands, it consisted of stems of shrubs and saw palmetto killed by the fire but not consumed by it. After about 5–6 years, these stems decayed and fell to the ground. Fire-killed standing dead stems were still prevalent in the four-year-old stand but not in the six- or eight-year-old stands. Replacing fire-killed stems in the standing dead category in older stands were dead stems and branches of shrubs and dead leaves of saw palmetto that had grown since the last fire.

All stands had substantial organic matter in the soil (Figure 4). The soils of the saw palmetto transects had much more organic matter than the other stands. Excluding saw palmetto transects, soil organic matter pools differed among the stands (ANOVA, $p < 0.001$), and a priori contrasts indicated that Stand 2 differed from the others ($p < 0.001$). Soil organic matter standing crops exceeded total aboveground biomass in Stand 2 ($p = 0.02$) and Stand 4 ($p < 0.001$), but did not differ in Stand 1 ($p = 0.71$) or Stand 3 ($p = 0.11$).

Biomass and Soil Chemistry

Soil nutrient pools (0–30 cm) of TKN, P, Ca, Mg, K, and Na differed among the stands ($p < 0.001$), and for each nutrient, the a priori contrast between Stand

Table 1. Aboveground biomass (g/m²) in the scrub stands

		Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw		Saw		
		Palmetto		Palmetto		
Stand Age (yr)		2	4	4	8	25
		(N=6)	(N=4)	(N=2)	(N=7)	(N=6)
Biomass Category		\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
		(SD)	(SD)	(SD)	(SD)	(SD)
<i>Aristida stricta</i>		3.3	6.8	6.5	27.4	—
		(8.2)	(7.9)	(9.2)	(53.8)	—
<i>Befaria racemosa</i>	leaves	18.3	0.8	—	—	—
		(44.9)	(1.5)	—	—	—
	stems	19.7	0.5	—	—	—
		(48.2)	(1.0)	—	—	—
Cyperaceae		0.2	—	—	—	0.7
		(0.4)	—	—	—	(1.6)
<i>Hypericum</i> spp.		—	3.0	—	—	—
		—	(6.0)	—	—	—
<i>Ilex glabra</i>	leaves	—	—	9.5	—	—
		—	—	(13.4)	—	—
	stems	—	—	10.5	—	—
		—	—	(14.8)	—	—
<i>Lyonia</i> spp.	leaves	40.7	42.8	13.5	51.9	47.0
		(77.4)	(38.4)	(19.1)	(66.6)	(75.2)
	stems	20.7	30.8	11.5	52.4	130.3
		(41.3)	(29.1)	(16.3)	(65.6)	(197.6)
<i>Myrica cerifera</i>	leaves	—	0.8	1.5	1.7	—
		—	(1.5)	(2.1)	(4.5)	—
	stems	—	1.0	2.5	1.7	—
		—	(2.0)	(3.5)	(4.5)	—
<i>Quercus chapmanii</i>	leaves	21.5	—	—	45.0	18.2
		(34.2)	—	—	(64.7)	(26.4)
	stems	15.5	—	—	91.7	36.3
		(29.9)	—	—	(166.2)	(68.1)
<i>Quercus geminata</i>	leaves	57.3	118.5	5.5	57.0	78.5
		(76.5)	(229.0)	(7.8)	(90.9)	(70.8)
	stems	64.3	171.5	8.5	143.0	264.5
		(106.6)	(333.7)	(12.0)	(226.0)	(247.2)
<i>Quercus myrtifolia</i>	leaves	156.2	104.0	4.5	148.0	153.0
		(127.4)	(131.6)	(6.4)	(148.0)	(39.8)
	stems	391.0	258.0	5.0	364.1	847.2
		(720.6)	(315.2)	(7.1)	(397.6)	(409.0)
	trunks	—	—	—	—	567.5
		—	—	—	—	(1,390.1)
<i>Serenoa repens</i>	leaves	99.3	368.3	444.0	328.6	66.3
		(112.9)	(377.1)	(39.6)	(370.0)	(111.6)
	stems	15.7	85.0	120.0	57.7	19.3
		(19.3)	(99.7)	(36.8)	(64.0)	(32.5)
	rhizomes	1,696.7	2,204.8	4,409.5	3,239.6	223.2
		(3,289.8)	(3,074.7)	(242.5)	(3,921.8)	(546.6)

Table 1. Continued.

		Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw			
		Palmetto	Palmetto			
Stand Age (yr)		2	4	4	8	25
		(N=6)	(N=4)	(N=2)	(N=7)	(N=6)
		\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
Biomass Category		(SD)	(SD)	(SD)	(SD)	(SD)
<i>Vaccinium myrsinites</i>		2.0	1.3	—	4.7	3.5
		(2.5)	(1.5)	—	(7.7)	(8.1)
<i>Vaccinium stamineum</i>	stems	—	—	—	—	60.3
		—	—	—	—	(147.8)
<i>Ximenia americana</i>	leaves	5.2	—	—	—	—
		(12.7)	—	—	—	—
	stems	41.3	—	—	—	—
		(101.2)	—	—	—	—
Miscellaneous herbs		—	—	2.5	26.0	—
		—	—	(3.5)	(52.6)	—
Total—Live Leaves		404.0	646.0	487.5	690.3	367.2
		(200.0)	(230.0)	(34.6)	(230.1)	(116.3)
Total—Live Stems		568.2	546.8	158.0	710.7	1,925.5
		(676.9)	(199.8)	(19.8)	(607.6)	(1,306.7)
Total—Live excluding		972.2	1,192.8	645.5	1,401.0	2,292.7
Saw Palmetto rhizomes		(766.7)	(93.7)	(54.4)	(675.8)	(1,296.2)
Total Live		2,668.8	3,397.5	5,055.0	4,640.6	2,515.8
		(3,037.4)	(3,115.9)	(297.0)	(3,523.9)	(1,341.5)
Standing Dead—Saw Palmetto		53.3	340.0	366.5	575.6	49.5
		(49.5)	(173.4)	(145.0)	(559.1)	(95.3)
Standing Dead—Other		809.5	318.0	21.5	132.3	519.7
		(1,032.1)	(346.7)	(30.4)	(162.7)	(308.4)
Total Standing Dead		862.8	658.0	388.0	707.9	569.2
		(1,028.6)	(314.7)	(175.4)	(452.9)	(334.0)
Litter		439.3	482.0	575.0	1,171.1	1,091.3
		(669.1)	(218.1)	(147.1)	(322.1)	(250.5)
Total Standing Dead		1,302.2	1,140.0	963.0	1,879.0	1,660.5
and Litter		(1,171.2)	(492.4)	(322.4)	(373.9)	(354.3)

2 and the other stands was significant ($p < 0.001$). Aluminum pools were not different among the stands ($p = 0.24$).

Concentrations of TKN, P, Ca, Mg, K, Na, and Al in live biomass showed no trends with time since fire for species present in all stands (Schmalzer and Hinkle 1987). Litter concentrations of P, Ca, Mg, and K appeared elevated in the two year old stand as did standing dead concentrations of K, and Mg (Schmalzer and Hinkle 1987). Tables of nutrient concentrations by species and stand are available from the authors on request.

Saw palmetto rhizomes contained considerable standing crops of N (Table 2). Standing dead and litter were also significant pools (Figure 5). Standing dead

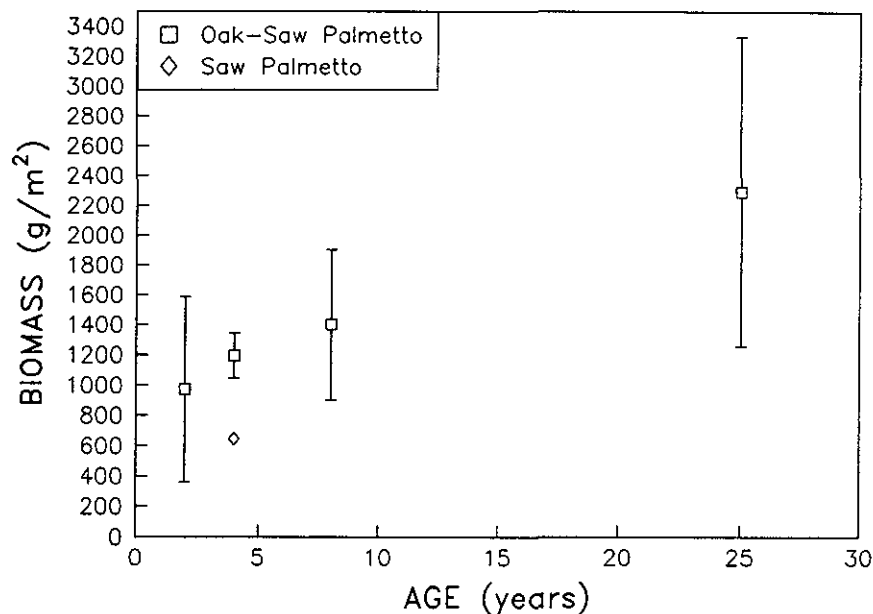


Figure 1. Standing crops of live biomass (excluding saw palmetto rhizomes) in the age sequence of scrub stands. Data shown are means and 95% confidence intervals for oak-saw palmetto scrub; means only are shown for the saw palmetto stand. The increase in live biomass with time is fit best by the equation $\log_{10} \text{ live biomass} = 0.391 \cdot \log_{10} \text{ age} + 2.758$, $r = 0.59$, $p = 0.002$.

was particularly important in the youngest stand. The stem biomass pool of N differed among stands ($p = 0.02$), but changes in leaf standing crops were not significant ($p = 0.11$). Accumulation occurred primarily in stem biomass in the oldest stand. The nutrient pool including saw palmetto rhizomes did not differ among stands ($p = 0.41$). Thus, increases in live biomass with time increased N standing crop, but only when saw palmetto rhizomes were excluded. TKN standing crops in living and dead biomass exceeded that in soil (0–30 cm) in Stand 3 ($p = 0.03$) but did not differ in Stands 1 and 4 ($p > 0.2$) (Figure 5). Stand 2, with greater organic matter in the soil, had much more N in the soil than the other stands and more in the soil than in biomass ($p = 0.002$).

Saw palmetto rhizomes, litter, and standing dead material contained major pools of P (Table 3). Saw palmetto rhizomes were a major pool in three of four stands where they had high biomass. The standing dead plus litter category did not differ among stands ($p = 0.22$). Phosphorus accumulated in live biomass with time since fire, primarily in stem tissue; stem standing crops differed among stands ($p = 0.04$), but not leaf standing crops ($p = 0.29$). However, P in total live biomass including saw palmetto rhizomes did not differ among stands ($p = 0.59$). Standing crops of P in living and dead biomass exceeded that in soil (0–30 cm) ($p < 0.001$) except in Stand 2 where they did not differ ($p = 0.4$) (Figure 6).

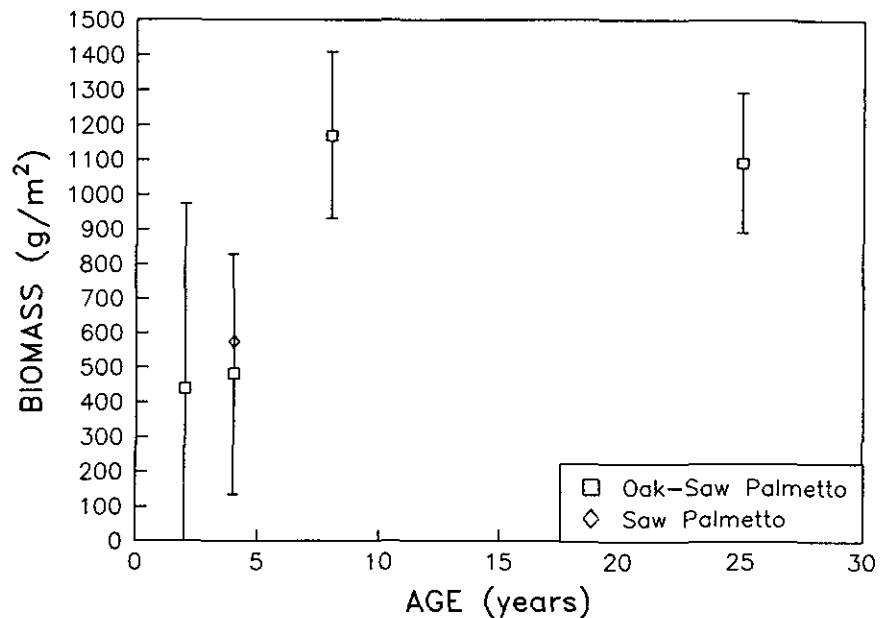


Figure 2. Standing crops of litter biomass in the age sequence of scrub stands. Data shown are means and 95% confidence intervals for oak-saw palmetto scrub; means only are shown for the saw palmetto stand. The increase in litter biomass with time is fit best by the equation $\log_{10} \text{ litter biomass} = 0.558 \cdot \log_{10} \text{ age} + 2.364$, $r = 0.60$, $p = 0.002$.

Stand 2 had much more soil P than the other stands probably due to greater soil organic matter.

Live stems, saw palmetto rhizomes, and standing dead plus litter were important pools of Ca (Table 4). The stem biomass pool differed among stands ($p = 0.03$), but not the leaf biomass pool ($p = 0.26$). Calcium accumulated in stem biomass in the oldest stand (Figure 7). Standing dead plus litter ($p = 0.05$) and total live standing crops ($p = 0.04$) differed among stands. Calcium standing crops in living and dead biomass exceeded that in soil (0–30 cm) in Stand 4 ($p < 0.001$); differences were not significant in Stand 1 ($p = 0.8$) and Stand 3 ($p = 0.6$) (Figure 7). Stand 2 had more Ca in the soil than in biomass ($p < 0.001$).

Saw palmetto rhizomes, litter, and standing dead were substantial pools of Mg in this system (Table 5). Pools in live leaves ($p = 0.008$) and live stems ($p = 0.04$) differed among stands. Stem biomass was most important in the oldest stand (Figure 8). The standing dead plus litter pool ($p = 0.1$) and the total including saw palmetto rhizomes ($p = 0.26$) did not differ among stands. Magnesium standing crops in living and dead biomass exceeded that in soil (0–30 cm) in Stand 4 ($p = 0.01$), pools were not different in Stand 1 ($p = 0.13$) and Stand 3 ($p = 0.19$), while soil was the greater pool in Stand 2 ($p = 0.008$) (Figure 8).

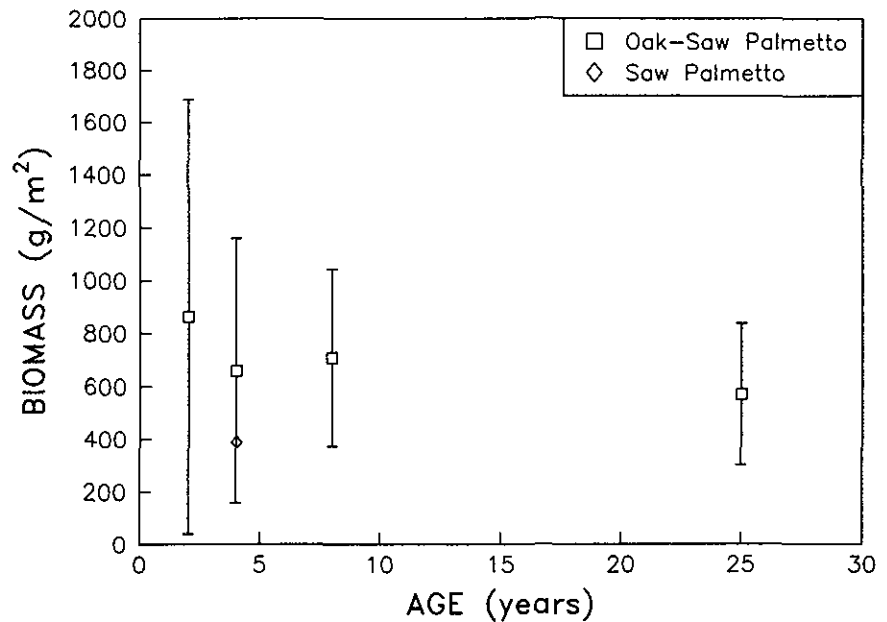


Figure 3. Standing crops of standing dead biomass in the age sequence of scrub stands. Data shown are means and 95% confidence intervals for oak-saw palmetto scrub; means only are shown for the saw palmetto stand. There is no significant trend with time ($r = 0.12$, $p = 0.56$).

Saw palmetto rhizomes were particularly important as a pool for potassium (Table 6, Figure 9). Potassium pools in leaves ($p = 0.24$), stems ($p = 0.15$), and total biomass ($p = 0.37$) did not differ among stands. However, the standing dead plus litter pool differed ($p = 0.01$). Potassium standing crops in living and dead biomass tended to exceed those in soil (0–30 cm) (Figure 9); however, these differences were not significant [Stand 1 ($p = 0.08$), Stand 2 ($p = 0.8$), Stand 3 ($p = 0.2$), Stand 4 ($p = 0.1$)].

Saw palmetto rhizomes were a substantial pool of Na (Table 7, Figure 10). Biomass pools in leaves ($p = 0.003$) and stems ($p = 0.01$) differed among stands, but standing dead plus litter ($p = 0.55$) or total biomass including saw palmetto rhizomes ($p = 0.38$) did not. Changes in leaf biomass Na were not directional with time (Table 7), but stem biomass accumulated Na with time. Standing crops of Na in living and dead biomass did not differ from that in soil ($p > 0.1$) for three of the four scrub stands. Stand 4, with little saw palmetto rhizome biomass, had more Na in soil than in biomass ($p = 0.01$).

Saw palmetto rhizomes and litter were the major biomass pools of Al; standing dead material contained smaller amounts (Table 8). Live biomass generally increased in importance as a pool with time since fire (Figure 11). Aluminum was in contrast to the other elements in that its standing crop in soil was much

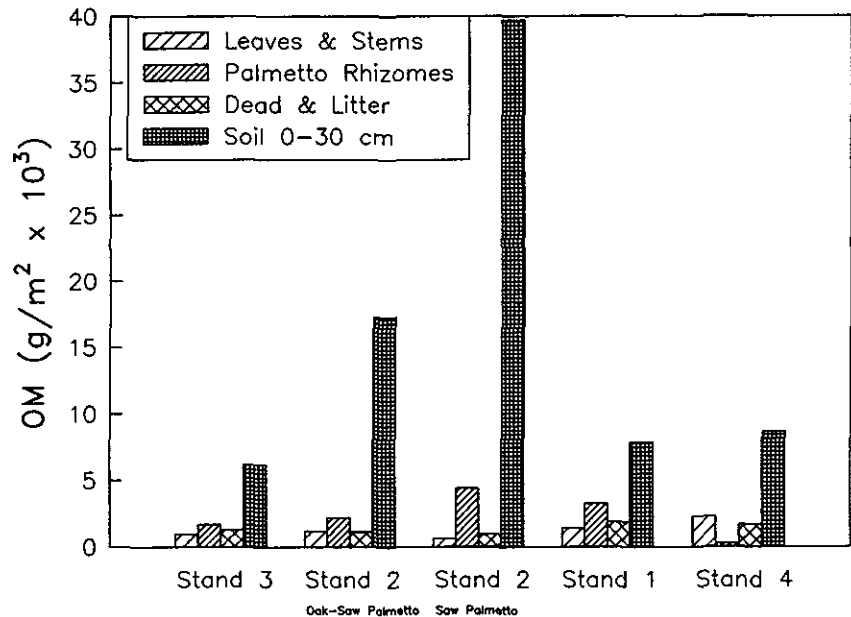


Figure 4. Comparison of organic matter in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

greater than that in living and dead biomass (Figure 11); these differences were significant ($p < 0.001$) in all stands.

DISCUSSION

Biomass

Live biomass (excluding saw palmetto rhizomes) in these stands was comparable to that of a variety of fire adapted shrublands (Table 9). Saw palmetto rhizomes contained considerable biomass in these stands (Table 9). Saw palmetto rhizomes are a unique element of the scrub community. They are generally unaffected by fire (Burton and Hughes 1961) forming a persisting element of aboveground biomass. Hilmon (1968) found length growth rates of saw palmetto rhizomes of 1.6–2.4 cm per year in south Florida; in south Georgia, the rate was about 1.2 cm per year. Abrahamson (1995) found saw palmetto rhizome growth rates of 0.6–1.1 cm per year in scrubby flatwoods and 0.8–2.2 cm per year in flatwoods of the Lake Wales Ridge. Thus, saw palmetto rhizomes one to several meters long have been growing for decades to centuries. Functionally, these rhizomes appear to combine elements of an aboveground stem with that of an underground root system, a situation with some parallels in the lignotubers of *Eucalyptus* species in the mallee scrub of Australia and other Mediterranean type shrublands (Walter 1979, James 1984). Christensen (1985) indicated that

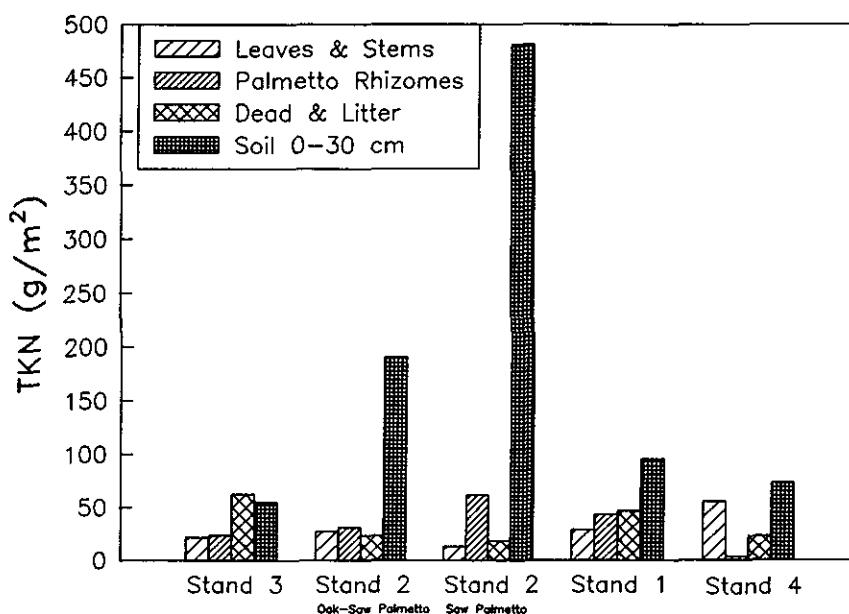


Figure 5. Comparison of total Kjeldahl nitrogen in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 2. Standing crops of total Kjeldahl nitrogen (TKN) ($\text{g/m}^2 \times 10^{-2}$) in above-ground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	953.64	1,369.25	973.85	1,474.05	930.73
Total—Live Stems	1,220.96	1,370.08	328.50	1,423.67	4,607.50
Saw Palmetto Rhizomes	2,375.40	3,086.70	6,173.30	4,535.40	312.43
Total Live (leaves, stems, rhizomes)	4,550.00	5,826.03	7,475.65	7,433.12	5,850.66
Standing Dead—Saw Palmetto	95.94	816.00	879.60	1,151.20	173.25
Standing Dead—Other	4,937.95	763.20	51.60	502.74	571.67
Litter	1,230.04	771.20	920.00	3,044.86	1,527.82
Total Standing Dead and Litter	6,263.93	2,350.40	1,851.20	4,698.80	2,272.74
Soil 0–15 cm	3,620.9	14,195.3	40,266.0	8,087.0	5,229.2
Soil 15–30 cm	1,882.6	4,890.8	7,807.4	1,468.4	2,070.9

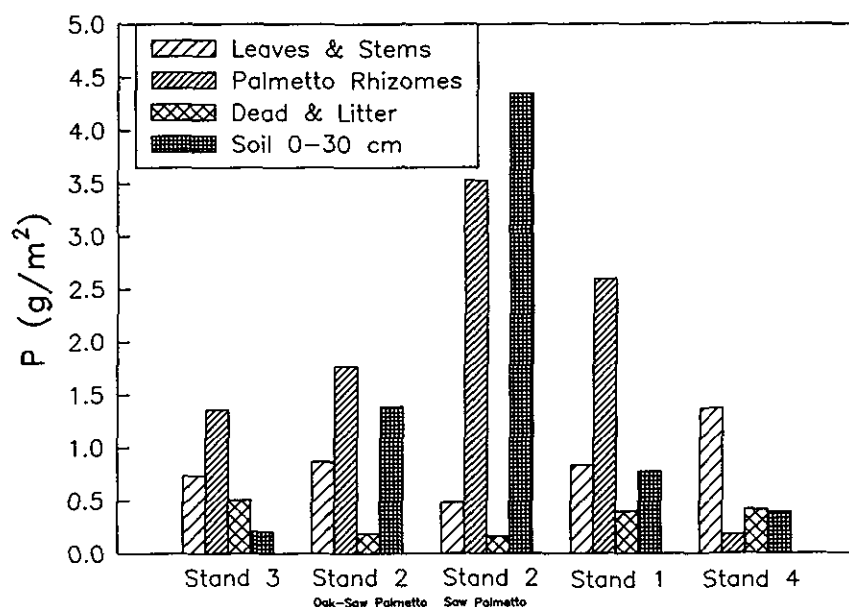


Figure 6. Comparison of phosphorus in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 3. Standing crops of total phosphorus ($\text{g/m}^2 \times 10^{-3}$) in aboveground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	362.88	522.50	377.01	457.21	358.50
Total—Live Stems	372.77	344.10	103.98	374.00	1,013.10
Saw Palmetto Rhizomes	1,357.36	1,763.84	3,527.60	2,591.68	178.56
Total Live					
(leaves, stems, rhizomes)	2,093.01	2,630.44	4,008.59	3,422.89	1,550.16
Standing Dead—Saw Palmetto	13.33	68.00	73.30	86.34	9.90
Standing Dead—Other	161.90	47.70	3.23	132.30	129.93
Litter	329.48	72.30	86.25	175.67	272.83
Total Standing Dead and Litter	504.70	188.00	162.78	394.31	412.66
Soil 0–15 cm	162.0	992.0	3,420.0	571.0	319.0
Soil 15–30 cm	45.0	396.0	929.0	203.0	68.0

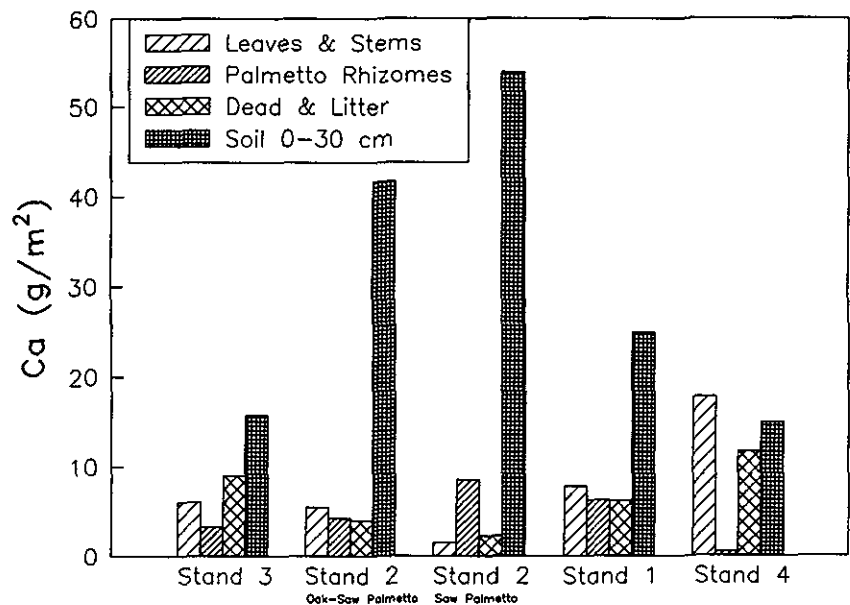


Figure 7. Comparison of calcium in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 4. Standing crops of calcium ($\text{g/m}^2 \times 10^{-2}$) in aboveground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	198.71	242.56	106.76	298.04	182.97
Total—Live Stems	409.74	308.49	47.28	485.46	1,588.87
Saw Palmetto Rhizomes	329.16	427.73	855.44	628.48	43.30
Total Live (leaves, stems, rhizomes)	937.62	978.78	1,009.48	1,411.99	1,815.15
Standing Dead—Saw Palmetto	4.42	49.64	53.51	69.07	5.15
Standing Dead—Other	512.41	220.69	14.92	85.47	326.89
Litter	382.63	134.96	161.00	468.44	832.66
Total Standing Dead and Litter	899.47	405.29	229.43	622.98	1,164.70
Soil 0-15 cm	985.1	3,149.6	3,997.8	2,004.3	991.4
Soil 15-30 cm	582.8	1,022.2	1,397.3	486.7	503.3

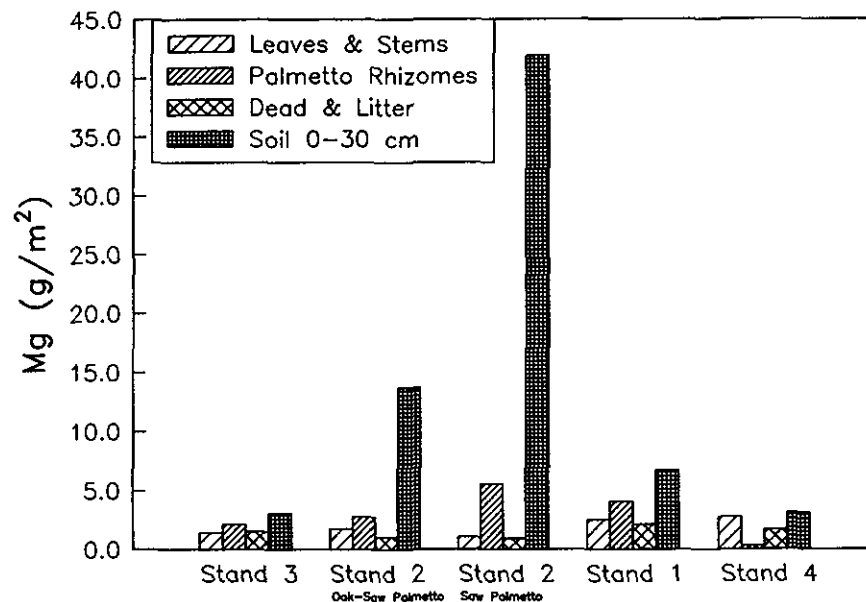


Figure 8. Comparison of magnesium in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 5. Standing crops of magnesium ($\text{g/m}^2 \times 10^{-3}$) in aboveground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	663.18	1,096.37	886.67	1,567.71	637.39
Total—Live Stems	771.88	658.10	183.81	961.98	2,135.20
Saw Palmetto Rhizomes	2,137.84	2,778.05	5,555.97	4,081.90	281.23
Total Live (leaves, stems, rhizomes)	3,572.90	4,532.52	6,626.48	6,611.59	3,053.82
Standing Dead—Saw Palmetto	60.23	377.40	406.82	754.04	46.04
Standing Dead—Other	825.69	248.04	16.77	138.92	571.67
Litter	654.56	433.80	517.50	1,241.37	1,080.39
Total Standing Dead and Litter	1,540.48	1,059.24	941.09	2,134.32	1,698.09
Soil 0–15 cm	2,198.0	9,895.0	33,131.0	5,769.0	2,335.0
Soil 15–30 cm	869.0	3,825.0	8,825.0	988.0	791.0

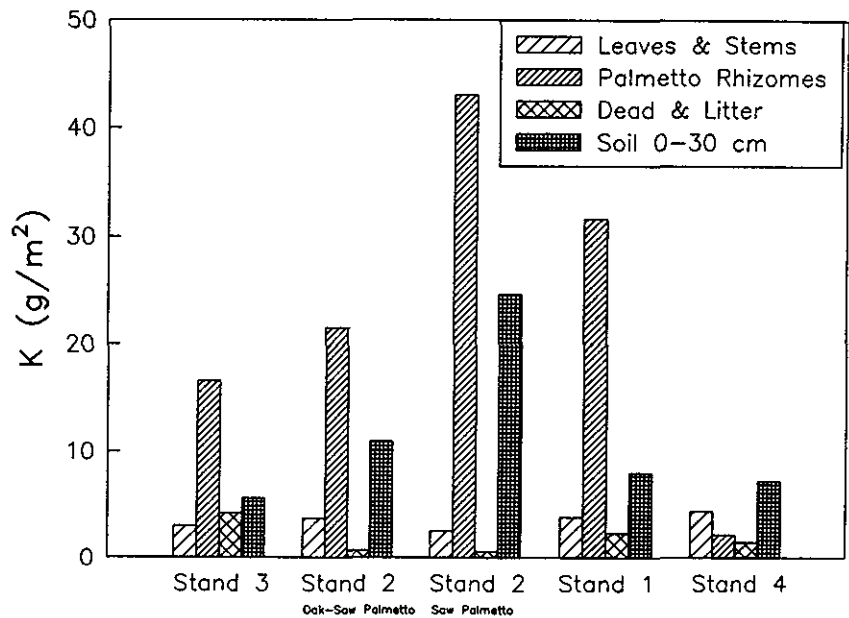


Figure 9. Comparison of potassium in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 6. Standing crops of potassium ($\text{g/m}^2 \times 10^{-3}$) in aboveground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	1,530.43	2,269.70	1,909.73	2,097.37	1,417.91
Total—Live Stems	1,488.72	1,428.30	630.43	1,739.15	2,956.65
Saw Palmetto Rhizomes	16,559.79	21,518.40	43,036.72	31,618.50	2,178.43
Total Live (leaves, stems, rhizomes)	19,578.91	25,216.40	45,576.88	35,455.01	6,552.99
Standing Dead—Saw Palmetto	90.08	363.80	392.16	1,485.05	64.85
Standing Dead—Other	3,416.09	181.26	12.26	58.21	410.56
Litter	716.06	168.70	201.25	784.64	1,004.00
Total Standing Dead and Litter	4,222.23	713.76	605.66	2,327.90	1,479.40
Soil 0–15 cm	3,339.0	7,088.0	19,098.0	5,728.0	5,360.0
Soil 15–30 cm	2,279.0	3,848.0	5,558.0	2,261.0	1,845.0

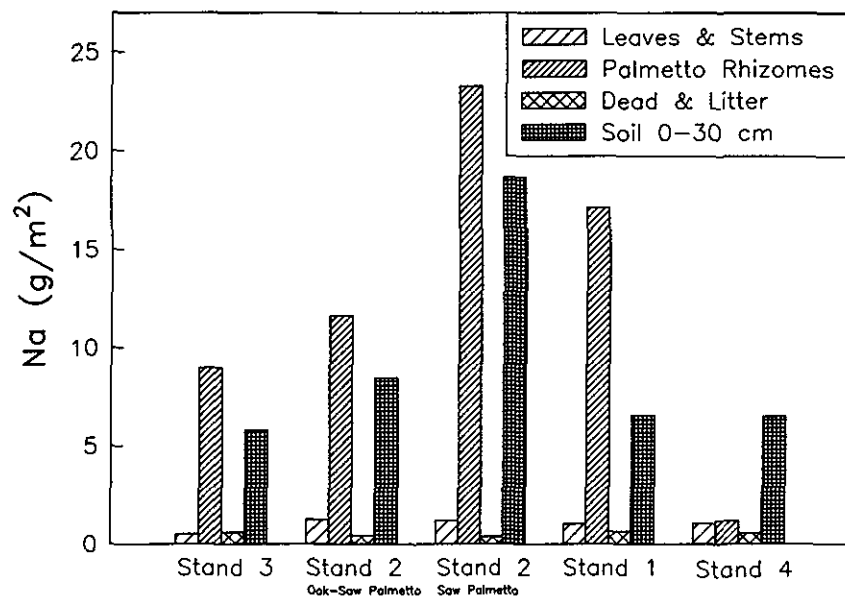


Figure 10. Comparison of sodium in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 7. Standing crops of sodium ($\text{g/m}^2 \times 10^{-3}$) in aboveground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	211.01	572.90	554.24	474.56	195.90
Total—Live Stems	298.74	662.00	629.39	537.83	841.80
Saw Palmetto Rhizomes	8,958.58	11,641.34	23,282.16	17,105.09	1,178.50
Total Live (leaves, stems, rhizomes)	9,468.32	12,876.24	24,465.79	18,117.49	2,216.20
Standing Dead—Saw Palmetto	26.12	159.80	172.26	310.82	23.27
Standing Dead—Other	388.56	124.02	8.39	35.72	233.87
Litter	188.90	154.24	184.00	304.49	305.56
Total Standing Dead and Litter	603.58	438.06	364.64	651.03	562.69
Soil 0-15 cm	2,983.0	4,752.0	11,705.0	3,629.0	3,683.0
Soil 15-30 cm	2,815.0	3,692.0	6,935.0	2,925.0	2,808.0

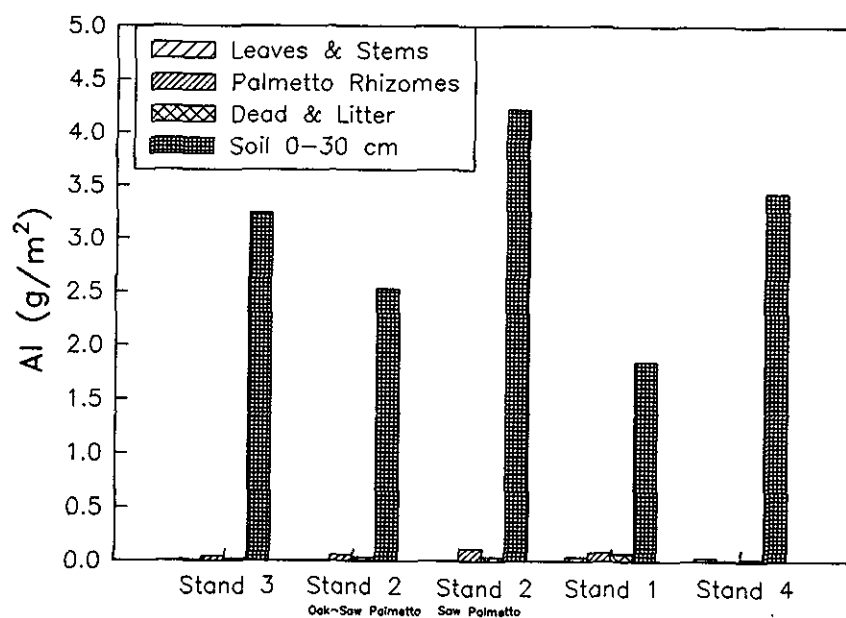


Figure 11. Comparison of aluminum in aboveground biomass and in soils of the scrub stands. Stand ages are Stand 3—2 yr, Stand 2—4 yr, Stand 1—8 yr, and Stand 4—25 yr. Saw palmetto transects of Stand 2 have a water table closer to the surface than the other stands.

Table 8. Standing crops of aluminum ($\text{g/m}^2 \times 10^{-4}$) in aboveground scrub vegetation and soil

	Stand 3	Stand 2	Stand 2	Stand 1	Stand 4
		Oak-Saw	Saw		
		Palmetto	Palmetto		
Stand Age (yr)	2	4	4	8	25
Biomass Category					
Total—Live Leaves	66.32	53.75	13.83	162.08	50.65
Total—Live Stems	38.44	25.94	21.36	228.40	247.63
Saw Palmetto Rhizomes	441.14	573.25	1,146.47	842.30	58.03
Total Live (leaves, stems, rhizomes)	545.90	652.94	1,181.65	1,232.78	356.32
Standing Dead—Saw Palmetto	1.60	17.00	18.33	115.12	5.94
Standing Dead—Other	48.57	9.54	0.65	15.88	51.97
Litter	175.72	322.94	385.25	597.26	163.70
Total Standing Dead and Litter	225.89	349.48	404.22	728.26	221.61
Soil 0-15 cm	12,780.0	8,780.0	28,440.0	12,290.0	16,690.0
Soil 15-30 cm	19,640.0	16,490.0	13,730.0	6,230.0	17,600.0

Comparison of biomass categories among selected shrublands

Biomass Type	Standing Crop (g/m ²)	Reference
l		
oak-saw palmetto rhizomes)	970-2,300	This Study
woods	1,050	Hough (1982)
	500-4,000	Wilbur and Christensen (1983)
shrub	1,440	Gray (1982)
subtropical	7,600	Gray (1982)
scrub	500	Boerner (1981)
is	1,000-2,000	Boerner (1981)
mes		
ds	220-3,210	This Study
	560	Hough (1982)
	440-1,200	This Study
is	1,860	Hough (1982)
postburn	530	Boerner (1983)
red	1,030	Boerner (1983)
	620-2,030	Gray (1982)
	570-860	This Study
postburn	570-750	Boerner (1981)
red	30	Boerner (1981)
	250-1,140	Gray (1982)

Stem tubers are common in shrublands where periodic, intense fire occurs and account for a considerable portion of shrub biomass.

Fire in oak-saw palmetto scrub was comparable to other systems but less than that reported for slash pine (*Pinus elliottii*)/live oak (*Ilex glabra*) vegetation (Hough 1982), perhaps because of the presence of live oak trees. Litter production and decomposition in oak-saw palmetto scrub appeared to reach equilibrium in about eight years. McNab (1981) reported that the forest floor loading of slash pine/palmetto stands increased within 3 years post-fire and then decreased to equilibrium at 20 years. The litter may account for the longer time to equilibrium.

Stem tubers formed a conspicuous element in these scrub communities. In the two year old stand, it was 89% of live biomass (excluding rhizomes) and at 25 years age it was 25% of live biomass. Large amounts of standing dead material after wildfire but

much less in unburned sites (Table 9, Boerner 1981). Some other shrublands (e.g., chaparral) accumulate considerable standing dead material. Christensen (1985) stated that the dead-to-live ratio increases with the time since fire in most shrub communities. In oak-saw palmetto scrub, the ratio of litter plus standing dead to total live (including saw palmetto rhizomes) was 48.8% in a two year old stand and 66.0% in a 25 year old stand. However, this is due in part to there being fewer saw palmetto rhizomes in the oldest stand sampled. Excluding saw palmetto rhizomes, the ratio decreased from 134% at two years to 72% at 25 years.

Belowground biomass was not measured in this study. *Quercus inopina* clones in scrub at Archbold Biological Station had about 70% of their biomass below ground (Johnson et al. 1986). Guerin (1988, 1993) found that *Quercus geminata* and *Quercus myrtifolia* clones (3–4 years since fire) in Ocala National Forest had about two-thirds of their biomass below ground. These root to shoot ratios are much higher than most forests (Santantonio et al. 1977). Belowground biomass data are available for few shrub communities. High ratios of below- to above-ground biomass have been reported in *Quercus gambelii* shrublands in the southwestern U.S. (Clary and Tiedemann 1986), in frequently coppiced *Quercus ilex* stands on xeric sites in southern France (Canadell and Roda 1991), and in Australian heathlands (Specht et al. 1958, Low and Lamont 1990). In California chaparral, Kummerow et al. (1977) found less biomass belowground than above.

Biomass and Soil Chemistry

Total Kjeldahl nitrogen concentrations used here (Schmalzer and Hinkle 1987) for leaves, stems, and rhizomes of saw palmetto, gallberry leaves and stems, standing dead material, and litter were greater than those reported by Hough (1982) for these components in the understory of slash/longleaf pine stands. TKN concentrations in scrub oaks (1.6–3.5%) were higher than those reported (0.5–1.0%) for oaks at Archbold Biological Station (Ann Johnson, Florida Natural Areas Inventory, pers. comm.). Scrub oaks in the southwestern U.S. had similar concentrations in leaves, e.g., *Q. gambelii*, 1.6% (Tiedemann and Clary 1985), *Q. turbinella*, 1.5%, (Klemmedson and Wienhold 1992), but lower concentrations in stems (0.5–0.8%). *Quercus ilex* leaves had concentrations of about 1.1–1.4% (Canadell and Vila 1992). Concentrations were in the general range reported for chaparral and coastal sage scrub species (Gray 1983) and various European ericads (Marrs 1978) but slightly higher than most shrub species in a northeastern oak-pine forest (Woodwell et al. 1975).

Other nutrient concentrations (P, Ca, Mg, K, Na) here were similar to levels reported previously for these species (Vickers et al. 1975, Hough 1982, A. Johnson pers. comm.). Similar concentrations have been reported for evergreen oaks (Canadell and Vila 1992, Klemmedson and Wienhold 1992), chaparral and coastal sage scrub species (Gray 1983), European ericads (Marrs 1978), oak-pine forest shrub species (Woodwell et al. 1975), and various Mediterranean shrubs (Specht and Moll 1983).

Standing crops of nutrients in live biomass in scrub were similar to those reported in other shrublands (Table 10), although N pools were relatively high

Table 10. Comparison of nutrient standing crops among selected shrublands

Biomass Type	Standing Crop (g/m ²)						Reference
	N	P	Ca	Mg	K	Na	
Aboveground—Live							
Scrub ¹	13.0–55.4	0.48–1.37	1.5–17.7	1.1–2.8	2.54–4.37	0.51–1.23	This Study
Chaparral	41.7	2.89	33.8	4.2	16.47	—	Gray (1983)
Coastal Sage	7.6	1.05	5.37	1.82	6.76	—	Gray (1983)
Scrub							
Various	3.4–41.1	0.14–2.9	—	—	—	—	Rundel (1983)
Shrublands							
Saw Palmetto Rhizomes							
Scrub	3.1–61.7	0.18–3.53	0.4–8.6	0.3–5.6	2.18–43.0	1.18–23.3	This Study
Pine Flatwoods	2.2	0.45	0.17	0.6	0.22	1.36	Hough (1982)
Standing Dead							
Scrub	7.4–50.3	0.08–0.22	0.7–5.2	0.4–0.9	0.48–3.51	0.18–0.41	This Study
Chaparral	6.3	0.46	5.6	6.7	2.68	—	Gray (1983)
Coastal Sage	1.1	0.08	0.75	0.15	0.63	—	Gray (1983)
Scrub							
Aboveground Live & Dead							
Pine Flatwoods	7.1	0.59	2.3	1.1	2.1	1.32	Hough (1982)
Understory							
Litter							
Scrub	7.7–30.4	0.07–0.33	1.3–8.3	0.5–1.2	0.17–1.0	0.15–0.31	This Study
Pine Flatwoods	14.7	0.11	6.0	1.0	2.1	0.3	Hough (1982)
Chaparral	20.5	0.60	26.1	6.7	4.7	—	Gray (1983)
Coastal Sage	4.7	0.4	8.9	3.1	1.8	—	Gray (1983)
Scrub							
Various	2.5–23.0	0.1–2.2	—	—	—	—	Rundel (1983)
Shrublands							

¹ Excluding saw palmetto rhizomes.

and K pools low. Nitrogen pools in live plus standing dead biomass of scrub exceeded those reported for slash pine flatwoods understory vegetation, but other nutrient pools were similar (Table 10). Saw palmetto rhizomes were important nutrient pools in scrub and larger than those reported for slash pine flatwoods (Table 10, Hough 1982). This was due primarily to greater saw palmetto biomass, except for N where concentrations in scrub were also greater. Litter biomass nutrient pools in scrub were comparable to similar shrublands (Table 10). Most nutrient pools in standing dead biomass in scrub were comparable to other shrublands, although N pools were higher (Table 10).

Aluminum concentrations were generally similar to those found by Vickers et al. (1975). Few studies report Al concentrations in vegetation. Hough (1982) reported larger pools of Al in litter (1.42 g/m²) but similar amounts in live understory biomass (0.07 g/m²) and saw palmetto rhizomes (0.05 g/m²) in slash pine flatwoods compared to oak-saw palmetto scrub.

There were no apparent effects of fire on nutrient concentrations in live biomass in the two year old stand. However, litter showed elevated K, Ca, and P in the youngest stand, possibly as the result of ash deposition from fire. Sodium was not increased; it is a more mobile ion and any deposited in ash may have leached by two years post-fire.

Soil chemical properties in scrub are strongly influenced by depth to the water table (Schmalzer and Hinkle 1992). Wetter soils have more organic matter, higher cation exchange capacity, and more nutrients. Effects of fire on scrub soils appear minor. Soil pH and Ca showed modest increases after a prescribed burn of some of these stands and there was a delayed increase in NO₃-N (Schmalzer and Hinkle 1991). Abrahamson (1984a) found a short-lived increase in Ca but little change in other soil parameters after fire.

Nutrient standing crops of N, P, Ca, Mg, and K in biomass equaled or exceeded those in the soil except in Stand 2. Only Al had consistently greater pools in soil than biomass. If scrub oaks have even half of their biomass below ground, then it is likely that the biomass pools of most biologically important elements exceed those in the mineral soil, except on wetter sites. Total soil cation nutrient levels probably exceeded available nutrient values used to calculate pool sizes here; however, these may be made available only slowly by weathering. In contrast, available soil N concentrations (NH₄-N + NO₃-N) were much less than total N (Schmalzer and Hinkle 1992).

Nutrient Cycling Considerations

Several properties of oak-saw palmetto scrub place it among those systems that could be vulnerable to nutrient losses from fire. Oak-saw palmetto scrub occurs on low nutrient soils, and much of the nutrient capital is sequestered in biomass rather than the mineral soil; therefore, it is an oligotrophic system (Boerner 1982). However, scrub species have evolved under regimes of low nutrient soils and repeated fires (Abrahamson 1984a, 1984b). These species have characteristics considered adaptations to low nutrient soils including evergreen, sclerophyllous leaves (Loveless 1961, 1962; Monk 1966). Other characteristics, particularly the dominance of sprouting species, are considered adaptations to repeated fires (Keeley and Zedler 1978, Malanson 1985).

Our data were not sufficient to determine vulnerability of scrub to nutrient loss, because it would be necessary to quantify belowground biomass and nutrient pools, volatilization and leaching losses with fire, and post-fire nutrient uptake. We can compare nutrient deposition from precipitation to see if it is important relative to biomass pools.

Nitrogen is the element most often lost in significant quantities with fire (Raison 1979). Inorganic nitrogen ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) deposition in precipitation ($0.262 \text{ g/m}^2\text{/yr}$) was minor compared to the biomass pools. Biological nitrogen fixation in scrub has not been studied. *Galactia elliotii* and *G. volubilis* are the only common legumes in these scrub stands. Nitrogen fixation is associated with wax myrtle (*Myrica cerifa*) (Permar and Fisher 1983); however, the low percent cover of wax myrtle (1–2%) suggests that nitrogen additions by it are minor. Non-symbiotic nitrogen fixation probably occurs in scrub as it does in slash pine plantations (DiStefano and Gholz 1989). Stimulation of nitrogen fixation after fire has been reported for loblolly pine (*Pinus taeda*) forests (Jorgensen and Wells 1971), but whether this occurs in scrub is unknown. Available nitrogen ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) was a small fraction of TKN in scrub soils (Schmalzer and Hinkle 1992), but it did increase 18 months after a fire (Schmalzer and Hinkle 1991).

Calcium deposition by precipitation ($0.145 \text{ g/m}^2\text{/yr}$) was small compared to total biomass pools. Calcium inputs were more significant compared to the amount of calcium in leaves and stems; calcium in saw palmetto rhizomes is not affected by fire. Calcium losses from fire were typically less than that of N, P, or K (Raison et al. 1985), and it is not as mobile in the soil as other cations; thus, precipitation may supply enough to replace the losses from fire. Magnesium in precipitation ($0.137 \text{ g/m}^2\text{/yr}$) was small compared to total biomass pools. Magnesium in leaf and stem biomass ($1.4\text{--}2.8 \text{ g/m}^2$) could accumulate from 10 to 20 years of precipitation. Potassium deposition by precipitation ($0.064 \text{ g/m}^2\text{/yr}$) was small compared to biomass pools. Potassium losses could occur since it is generally more mobile in the soil than Ca or Mg. In contrast, precipitation deposition of Na ($1.082 \text{ g/m}^2\text{/yr}$) was relatively large compared to biomass pools and losses of it could be replaced more readily.

Additions of major nutrients by precipitation were small relative to biomass pools, suggesting that efficient nutrient accumulation, retention, and recycling are important to maintaining the stability of the system (Raison 1979). Nitrogen fixation appears to be required to replace N lost in scrub fires. Nutrient uptake by plants or immobilization in the soil may be important in limiting the losses of cations and P as has been found in low nutrient ecosystems such as the New Jersey Pine Barrens (Boerner 1983) and tropical pine savannas (Kellman et al. 1987). Saw palmetto rhizomes are an important nutrient pool that persists through fires. Although nutrients tended to accumulate in stem biomass with time, total biomass pools for N, P, Mg, and Na were not different among stands when saw palmetto rhizomes were included. The persistence of standing dead material may be another nutrient retention mechanism (Boerner 1983).

SUMMARY

1. Live biomass increased with time since fire. Litter biomass increased for about eight years post-fire. Standing dead biomass and saw palmetto rhizomes

were important biomass components. Biomass in oak-saw palmetto scrub was similar to that in chaparral and other shrublands.

2. Nutrients concentrations in live biomass did not change with time since fire. Nutrient concentrations in biomass and nutrient standing crops were similar to those in other shrublands.

3. Soil chemical properties were strongly influenced by soil drainage; the wetter soils had more organic matter and larger standing crops of nutrients.

4. Biomass pools of major nutrients (N, P, K, Ca, Mg, Na) frequently equaled or exceeded those in the soil. Concentration of nutrients in biomass could increase vulnerability to nutrient losses. However, the importance of standing dead biomass, saw palmetto rhizomes, and probably belowground biomass as nutrient pools may buffer the system against nutrient losses.

5. Deposition rates of N, P, Ca, Mg, and K in precipitation were low compared to biomass pools, while deposition of Na was greater relative to amounts in biomass. Nitrogen fixation and mechanisms that retain and recycle nutrients may be important to the persistence of scrub on low nutrient soils.

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